THE
AMERICAN NATURALIST

VOL. XLVII *August, 1913* NO. 560

GENETICAL STUDIES ON ŒNOTHERA. IV

THE BEHAVIOR OF HYBRIDS BETWEEN *Œnothera biennis* AND *Œ. grandiflora* IN THE SECOND AND THIRD GENERATIONS[1]

DR. BRADLEY MOORE DAVIS

UNIVERSITY OF PENNSYLVANIA

THOSE who have followed the reports of my genetical studies on *Œnothera* (Davis, '10, '11 and '12*a*) must have noted that I have obtained during the past four years a series of hybrids from the cross *grandiflora* × *biennis* with various points of strong resemblance to forms of *Œnothera Lamarckiana* De Vries. I say forms of *Œ. Lamarckiana* because it is, I think, clear (Davis '12*a*, p. 383) that this species has within itself a number of biotypes which, although in most respects essentially similar, differ from one another in the size of the petals, in the height of the stigma relative to the tips of the anthers, and, to a lesser degree, in some other characters. These biotypes may be segregated by critical selection and cultivation through pure lines and I venture to believe that the *Lamarckiana* of De Vries's cultures was less pure when he began his studies twenty-five years ago than it is to-day. At the present time a very large-flowered type (petals 4–4.5 cm. long) is generally thought

[1] An abstract of this paper was presented before the American Society of Naturalists at its meeting in Cleveland on January 2, 1913.

of when this plant is discussed. *Lamarckiana* then, like many species, has its minor strains which may be isolated.

Heribert-Nilsson ('12) in his recent extended analytical studies on *Œ. Lamarckiana* reaches the same conclusion that *Lamarckiana* is not a simple species but, on the contrary, polymorphic. His investigations are the first serious attempts to bring forward evidence that will explain the "mutants" and minor varieties as derivatives from a hybrid through the segregation and recombination of characters on Mendelian principles. These studies form a very important contribution to the research upon this interesting plant.

I have not as yet among my hybrids of *biennis* and *grandiflora* obtained any plant that matches in all respects any one of the biotypes of *Lamarckiana*. On the other hand, there is, I believe, no important character of taxonomic value presented by *Lamarckiana* through its various biotypes that has not appeared in some of my hybrids. I have, as it were, surrounded the group of *biotypes,* which we call the species *Lamarckiana,* with a circle of hybrids that in various characters agree with the plants that have come down to us through the cultures of De Vries. If the group of biotypes of *Lamarckiana* is enlarged to include certain of its so-called "mutants" the number of my hybrids with points of resemblance to this larger assemblage is correspondingly increased.

My studies have now reached a stage where I have data to present on the behavior of hybrids between *biennis* and *grandiflora* in the F_2 and F_3 generations. These later hybrids have a two-fold interest; first with respect to their possible interpretation in relation to Mendelian principles of inheritance, and second, with respect to the behavior of certain types in the F_2 generation, which types repeat in the F_3 the history of the F_1 parent hybrid in throwing the same marked variants, and thus exhibit a behavior similar to that of *Lamarckiana* when

in successive generations it produces a series of similar "mutants."

There has come to light during the past year a historical matter of interest which bears very directly on the problem of the origin of the *Lamarckiana* of De Vries's cultures. This is the determination of Lamarck's plant, *Œnothera Lamarckiana* Seringe (1828), grown in Paris at about 1796 or somewhat earlier, as a form of *Œ. grandiflora* Solander (1789) = *Œ. grandiflora* "Aiton." The evidence for this determination (see Davis, '12*b*) is very convincing and there can be, I think, no doubt but that De Vries ('01, Vol. I, pp. 316, 317) was mistaken when he identified the material of his cultures with the type specimen of *Œ. Lamarckiana* Seringe, the sheet upon which Lamarck (?1798) based his description in the Encyclopédie Méthodique Botanique. It should be remembered that Professor De Vries made this identification some years before the rediscovery of *Œ. grandiflora* at its original habitat in Alabama in 1904, and consequently before there was available our present information on this species.

Œnothera Lamarckiana Seringe (1828) now becomes a synonym of *Œ. grandiflora* Solander, described in Aiton's "Hortus Kewensis" (1789), and the material of De Vries's cultures can not bear the name *Lamarckiana* with Seringe as an authority. I have suggested, however, in the paper cited above (Davis, '12*b*, p. 530) that the plant of De Vries's cultures retain the name *Lamarckiana* to be written in the form *Œ. Lamarckiana* De Vries. A change of name for this plant would be most unfortunate, since it would result in endless confusion in the literature of experimental morphology. The evidence indicates that *Œ. Lamarckiana* De Vries has come to us as the product of the garden through a long history of cultivation and that its parentage is far from pure; in short, that it is of hybrid origin. As a garden plant we are seemingly justified in giving it the name *Œ. Lamarckiana* De Vries by Article 50 of the code

formulated by the International Botanical Congress held in Vienna in 1905.

The effect of the separation of *Œ. Lamarckiana* De Vries from Lamarck's plant of about 1796 is to make far more tangible the problem of its origin. In former papers in the NATURALIST (Davis, '11, p. 226; '12, p. 379) I have criticized adversely the attempts that have been made to place the appearance of *Lamarckiana* De Vries in Europe at dates previous to 1778 when *Œ. grandiflora* Solander was introduced at Kew. In a recent contribution Gates ('13, pp. 17–19) admits that the presence of *Lamarckiana* in Europe previous to 1760 is not established and thus abandons his former position when he sought to prove its very early introduction from America. With Lamarck's plant (*Œ. Lamarckiana* Seringe) removed from the discussion we are brought to periods where we may hope for more direct evidence on the history of *Lamarckiana* De Vries than that furnished by old accounts and figures. This matter will be further discussed at the end of this paper in the section entitled, "The Problem of the Origin of *Œ. Lamarckiana* De Vries."

The material of this paper will be arranged under the following headings: (1) F_3 Generations in the Family from the F_1 Hybrid 10.30*La,* (2) F_3 Generations in the Family from the F_1 Hybrid 10.30*Lb,* (3) Hybrids of *grandiflora B* × *biennis D* in the F_2 Generation, (4) A Discussion of the Behavior of the Hybrids in the Second and Third Generations with Reference to the Stability of Mendelian Factors, (5) The Habit of "Mutation" in *Œ. Lamarckiana* De Vries considered with Reference to the Behavior of the Hybrids between *biennis* and *grandiflora,* (6) The Problem of the Origin of *Œ. Lamarckiana* De Vries.

1. F_3 Generations in the Family from the F_1 Hybrid 10.30*La*

The F_1 hybrid plant designated 10.30*La* has already been described and figured (Davis, '11, pp. 211–213, Figs. 9, 10, 11), and a brief account of its F_2 generation was given in my last paper (Davis, '12*a*, pp. 410–413). The plant was the result of the cross *grandiflora B* × *biennis A*, the latter parent being a rather small-flowered race of *biennis* from Woods Hole, Massachusetts. The F_2 generation from 10.30*La* consisted of 1,451 plants, among which could be readily selected at an early stage of development a group of 141 rosettes much smaller than those constituting the mass of the culture and sharply distinguished by their strongly etiolated leaves of a narrower form. From these etiolated rosettes developed a class of dwarfs, the later foliage of which outgrew the etiolated peculiarities of the young plants and became green. The normal green rosettes constituting the mass of the culture presented a remarkable range of form, but inclined more towards the female parent of the cross, *grandiflora B*.

A large proportion of the plants, at maturity, were fairly close to the F_1 hybrid plant 10.30*La*, but there was presented a wide variation from this form with a markedly greater tendency towards the *grandiflora* parent type. Although the range of variation clearly indicated a process of segregation in this F_2 generation, it was a segregation modified by a general progressive advance in the size of the plant organs. Thus, with respect to flower size, the culture gave a large number of plants (about 50) with flowers as large as or larger than the *grandiflora* parent, while the smallest flowers represented were 2–4 times larger than those of the *biennis* parent. The leaves throughout the mass of the culture were, as a whole, larger than those of the parents of the cross and generally distinctly crinkled.

It should be recalled (see Davis, '12*a*, p. 412) that a

number of remarkable forms appeared in the F_2 culture in addition to the segregates, forms which no taxonomist would think of relating to either parent of the cross or to the F_1 hybrid plant 10.30*La*. Some of these forms were sterile, but the 141 peculiar dwarfs from etiolated rosettes and the extreme types showing progressive evolution were fertile, as was the culture, as a whole.

The problem which I outlined for study through the F_3 generation was two-fold: (1) Would extreme types of the F_2, such as the dwarfs, hold their characteristics, and (2) Would a selfed plant representative of the mass of the F_2 produce an F_3 progeny with points of similarity to the F_2 generation? If this proved true there would be presented a behavior analogous to that of *Lamarckiana*

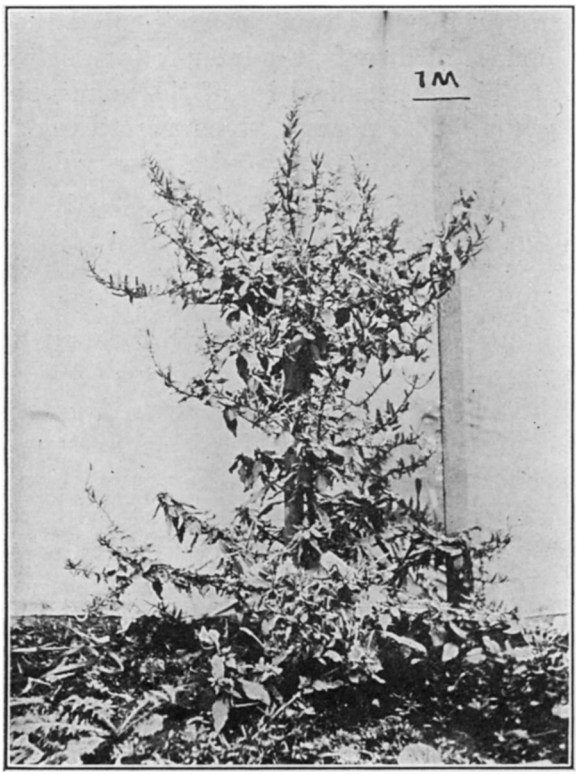


FIG. 1. Dwarf, 11.41*ra*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora* $B \times$ *biennis* A. This plant came from an etiolated rosette and shows the irregular branching characteristic of these dwarfs.

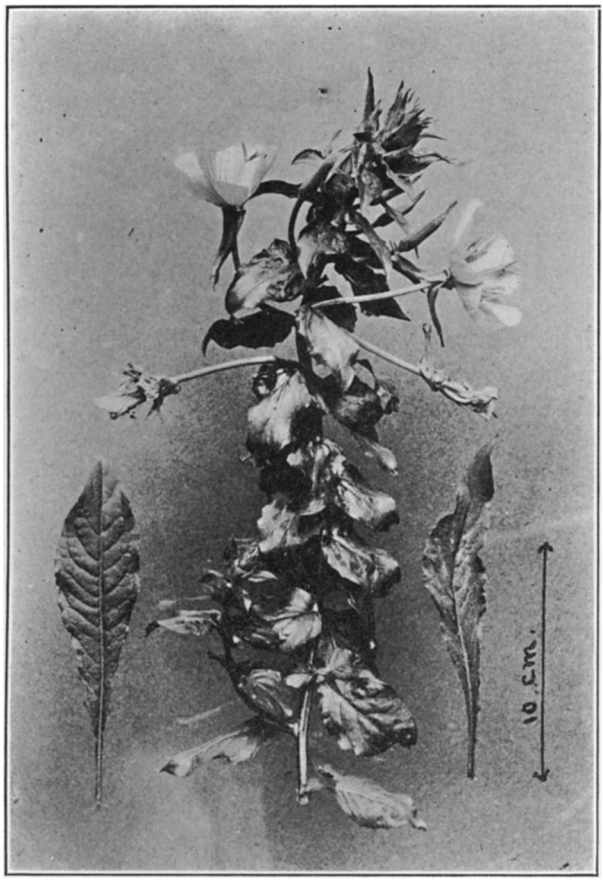


FIG. 2. Dwarf, 11.41*ra*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora* $B \times$ *biennis* A. The inflorescence and two leaves from the lower portion of the plant illustrate the varied forms of the leaves.

which throws off in successive generations marked variants which hold true when self-fertilized.

A plant, 11.41*ra*, was selected as being representative of the F_2 dwarfs from etiolated rosettes (Davis, '12*a*, p. 413) and, being selfed, became the parent of an F_3 generation (culture 12.53). The stunted growth and irregular branching characteristic of these dwarfs was well illustrated by this plant, 11.41*ra* (Fig. 1), as was also the varied form of the leaves (Fig. 2). The peculiarities of the etiolated rosettes from which the dwarfs come are well shown by the two plants at the bottom of Fig. 4.

From the F_2 dwarf, 11.41*ra*, 243 seeds, the contents of a single selfed capsule, were sown (culture 12.53). These produced 116 seedlings, the leaves of which, following the cotyledons were strongly etiolated in the lower half in the manner characteristic of these dwarfs; 69 rosettes were potted and carried to an advanced stage of development; 48 plants were brought to maturity. The rosettes were all etiolated, in some cases over three fourths of the basal portion of the leaves, in others somewhat less; the leaves were narrow and long-petioled. The F_3 generation (culture 12.53), from the F_2 dwarf, 11.41*ra*, was then absolutely true to the characters of the etiolated rosettes, one of which is shown in Fig. 4, 12.53*a*. The 48 plants brought to maturity presented the dwarf habit with ir-

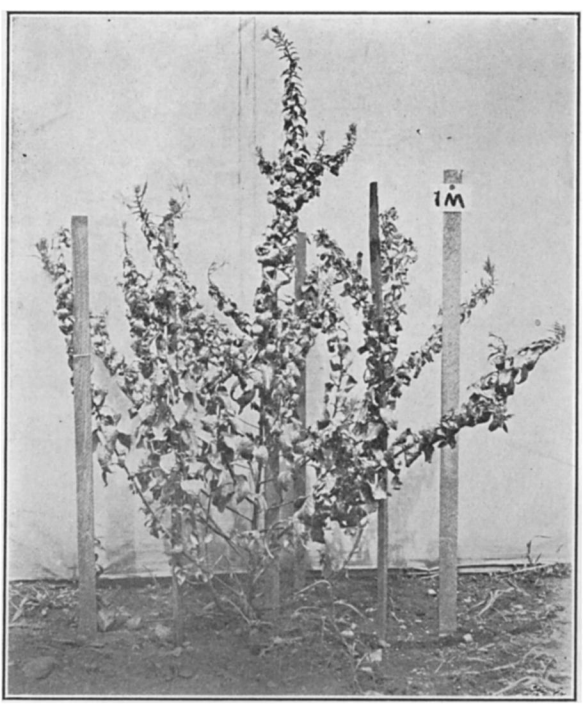


FIG. 3. A type, 11.41*c*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora* $B \times$ *biennis* A. This plant represented closely the character of the mass of the F_2 generation and was similar to the F_1 parent 10.30*La* except for a progressive advance in leaf and flower size.

regular branching and varied leaf form characteristic of the F_2 parent, 11.41*ra*; these plants also outgrew later the etiolated peculiarities of their rosettes. The flower size among these 48 plants of the F_3 varied greatly, a further point of similarity to the group of dwarfs in the F_2 generation. It appears then, as far as this culture in the F_3 gives evidence, that the dwarfs from etiolated

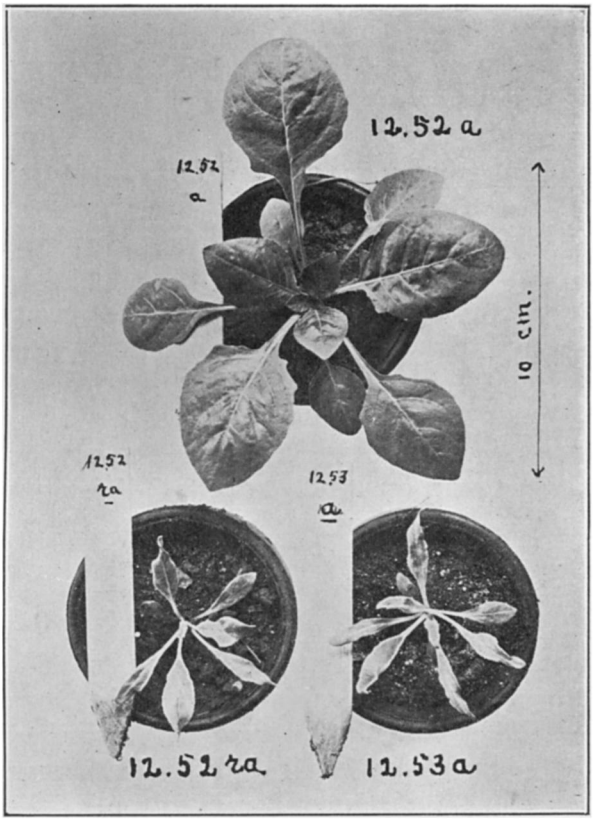


FIG. 4. 12.52*a* and 12.52*ra*, rosettes in the F_3 from the F_2 plant 11.41*c* (Fig. 3), the first, representative of the green rosettes constituting the mass of the culture, the second, one of 18 etiolated rosettes that developed into dwarfs. 12.53*a*, one of the etiolated rosettes in the F_3 from the F_2 dwarf 11.41*ra* (Figs. 1 and 2); it holds perfectly the characters of its F_2 parent, and is shown for comparison with 12.52*ra*.

rosettes in the F_2 generation constitute a group of plants very stable and perhaps homozygous with respect to their most striking peculiarities.

The second part of my study of this family concerned the behavior in the F_3 of a plant representative of the mass of the F_2 generation. The individual chosen, 11.41*c* (Davis, '12*a*, p. 412), was a large plant (Fig. 3) with long branches from the base and a foliage of conspicuously crinkled leaves. The type was represented by about 170 plants in the culture and, intergrading with other forms, stood close to the center around which the mass of the culture varied. This plant, 11.41*c*, was similar to the F_1 parent hybrid, 10.30*La*, except that it showed something of the general progressive advance throughout the F_2 generation in the broader and more crinkled leaves and in the somewhat larger flowers (petals 2.5 cm. long).

From the plant 11.41*c* an F_3 generation was grown (culture 12.52). There were sown 411 seeds, the contents of 3 selfed capsules and 285 rosettes developed. Among the seedlings 18 plants at once caught my attention as having etiolated leaves following the cotyledons. These 18 seedlings developed into small rosettes with narrow, strongly etiolated leaves, which could not be distinguished from the etiolated dwarfs that have been described above. The contrast between the green rosettes of this culture, 12.52, and these etiolated dwarfs, is illustrated in Fig. 4, which shows sister plants, 12.52*a* green and representative of the mass of the culture, and 12.52*ra* one of the 18 etiolated dwarf types. By the side of 12.52*ra*, for comparison (see Fig. 4), is shown one of the 48 etiolated dwarfs in culture 12.53, which, although an F_3 individual from 11.41*ra*, illustrates accurately the appearance of the etiolated dwarfs in the F_2 generation. It will be noted that the two dwarfs, 12.52*ra* and 12.53*a*, are of the same type.

The 18 etiolated rosettes of the F_3 culture 12.52 grew into dwarfs indistinguishable in all essentials from the 48 plants of the F_3 generation 12.53 and the 141 plants in the F_2 represented by 11.41*ra* (Figs. 1 and 2). They outgrew the etiolated condition of the younger stage, but re-

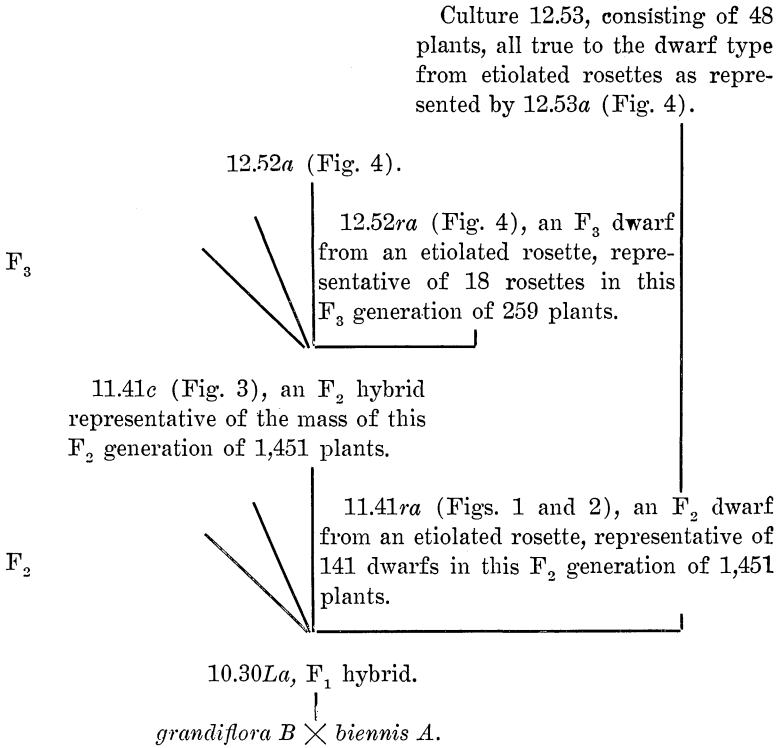
mained dwarfs, branching irregularly and presenting varied forms of leaves; there was also exhibited the same wide range of flower size. The evidence was then clear that in this family an F_2 plant of a type close to the mass of the F_2 culture could throw off in the F_3 the same class of dwarfs that appeared in the F_2 generation.

The normal green rosettes constituting the mass of the culture 12.52 (see Fig. 4, 12.52*a*) inclined strongly towards the *grandiflora* parent of the cross, but presented broader leaves not so strongly cut at the base. There was a wide range of variation among the rosettes, and forms appeared with narrow leaves which developed into plants with a foliage markedly different from the mass of the culture. The mass of the culture presented the same evidence of progressive evolution which was shown in the F_2 generation, *i. e.*, the leaves were large and crinkled as in the F_2 parent plant 11.41*c*, and there was likewise maintained the same advance in the size of the flowers, which ranged from types as large as or larger than the *grandiflora* parent to types as small as that of the F_1 hybrid 10.30*La*. In short, this F_3 generation, culture 12.52, from a plant 11.41*c*, fairly representative of the mass of the F_2, repeated the performance of the F_2 in exhibiting a large class of the same type of dwarf from etiolated rosettes and also repeated very much the same range of variation in leaf and flower characters shown by the F_2 generation. There was then presented a behavior closely parallel to that of *Lamarckiana* when it throws off in successive generations the same marked types of variants, which hold true.

Late in the season two plants were noted (12.52*fa* and 12.52*fb*) upon which a large number of flowers were 5-merous, *i. e.*, the flowers had 5 sepals, 5 petals, 10 stamens, and as far as noted 5 cells in the ovary. I am not aware that this character has before been noted in the genus *Œnothera*. These flowers were not restricted to particular branches and were found in the same inflorescence with normal flowers. The 5-merous flowers, were not ob-

served by me until October, too late in the season to self-pollinate with the hope of obtaining seed. Open-pollinated seed was, however, collected from these two plants and will be sown in the hope that this interesting sport may be followed in later generations.

The genealogy of the family from the F_1 hybrid 10.30*La*, in so far as it refers to the production of dwarfs, is presented in outline as follows:



2. F_3 Generations in the Family from the F_1 Hybrid 10.30*Lb*

The F_1 hybrid designated 10.30*Lb* was a sister plant to 10.30*La* and, therefore, also the product of the cross *grandiflora B* × *biennis A*. It has been described and figured in the earlier paper (Davis, '11, pp. 213–216, Figs. 12, 13 and 14), and a brief account of its F_2 generation

will be found in my last contribution (Davis, '12*a*, pp. 413–415). From the F_2 generation of 992 rosettes, culture 11.42, a group of 147 were sharply distinguished by their uniformly small size and narrow leaves. These developed into a class of very remarkable dwarf plants (Davis, '12*a*, p. 415, 11.42*r*) which at maturity were from 3–4 dm. high, rarely branched, and bore medium-sized flowers (Fig. 5). The leaves of the rosettes and mature plants were fully green; there was no etiolation so characteristic of the group of dwarfs from the sister F_1 hybrid 10.30*La*. The character of the young dwarf rosettes is shown in Fig. 7 and Fig. 9, 12.59*a*, in comparison with rosettes (shown above) similar to forms representative of the mass of the culture.

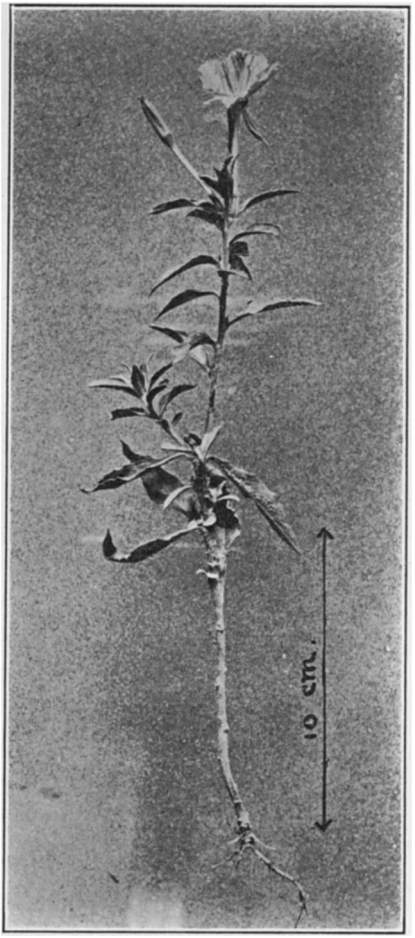


FIG. 5. Dwarf, 11.42*r*, in the F_2 from the F_1 plant 10.30 *Lb*, hybrid of *grandiflora B* × *biennis A*. This plant came from a rosette similar to that shown in Fig. 7, 12.59*a*.

The rosettes constituting the mass of the culture exhibited a wide range of form with the extremes approaching the rosettes of the *biennis* and *grandiflora* parents; there was not shown a clearly defined tendency towards either parent of the cross. From these rosettes a much more varied culture developed than the F_2 generation from the plant 10.30*La*.

There was more evidence of segregation towards the respective parents, but the same progressive advance in flower size. Many plants bore flowers as large as or larger than those of the *grandiflora* parent, while no plant presented flowers as small as those of the *biennis* parent. The foliage was extremely varied, ranging from lanceolate leaves to broadly elliptical or ovate leaves with well-defined crinkles.

A larger number of remarkable forms appeared in this culture, 11.42 (see Davis, '12*a*, p. 415), than in the one from the plant 10.30*La*, forms that would rank as types specifically distinct from either parent of the cross and from the F_1 hybrid plant 10.30*Lb*. Among these we shall refer to (1) the dwarf type 11.42*r* (Fig. 5), (2) a small-leaved type 11.42*f* (Fig. 6), (3) a large-flowered type with large crinkled leaves 11.42*g* (Fig. 8), rather common and fairly representative of the mass of the culture, (4) a medium-flowered type remarkable for its broad-much-crinkled leaves 11.42*l* (Fig. 14), and (5) a plant with very narrow leaves and very small flowers, anthers sterile 11.42*j* (Fig. 15).

The same problem lay before me in the study of the F_3 generations from these types in the F_2 of the plant 10.30*Lb*, as in the family which has just been described from the sister plant 10.30*La*. Would the extreme types such as the dwarfs hold their characters, thus proving to be homozygous, and would selfed plants more or less representative of the mass of the F_2 repeat in their F_3 generations something of the history of the F_2?

Of the 147 dwarf rosettes in the F_2 from 10.30*Lb* there were brought to maturity 90 plants. These constituted, as stated above, a very uniform group with characters well shown in Fig. 5. One of these, 11.42*ra*, was selected and selfed to become the parent of an F_3 generation. The contents of one capsule, 196 very small seeds, were sown and gave culture 12.59, comprising 66 rosettes, all similar and dwarf. One of these rosettes is shown in

Fig. 7 and Fig. 9, 12.59*a*, and it should be noted that the specimen is not a seedling, but a half-grown rosette comparable in point of age to the large rosettes (shown above) which represent closely the normal form and size. The dwarfs are delicate plants, very sensitive to drought, and I was able to bring only 46 individuals to maturity. These proved to be in all respects similar to the dwarfs of the F_2 generation, except that they were even smaller in stature and flower size; this further dwarfing was, however, probably due to less favorable cultivation. From the behavior of this F_3 we may, I believe, safely conclude that the dwarfs of the F_2, representing an extreme type, are stable, or homozygous, with respect to their most important characteristics.

There will now be described the F_3 generation from a small-leaved plant, 11.42*f* (Fig. 6), about 1 m. high, with

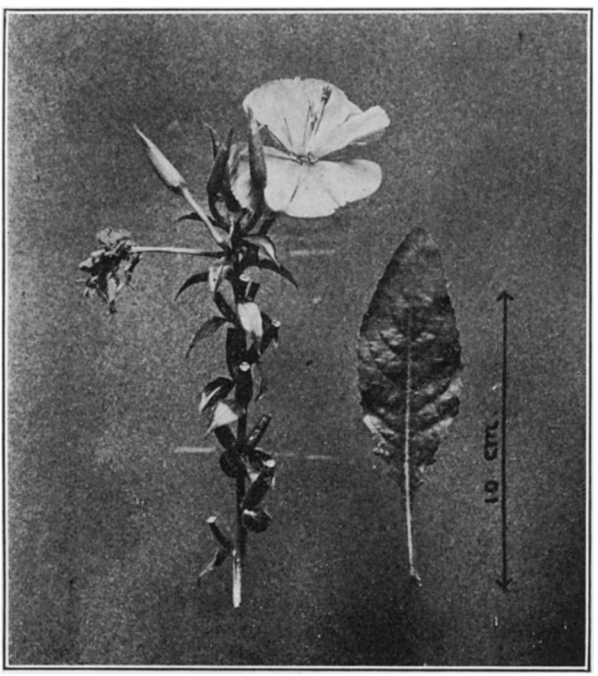


FIG. 6. A type, 11.42*f*, in the F_3 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*. A form characterized by small leaves, medium-sized flowers, and large capsules.

medium-sized flowers and large capsules (3.3 cm. long). This type (Davis, '12*a*, p. 415, 11.42*f*) was represented by several plants in the F_2 from 10.30*Lb*. It illustrated an extreme combination of small leaves with large capsules,

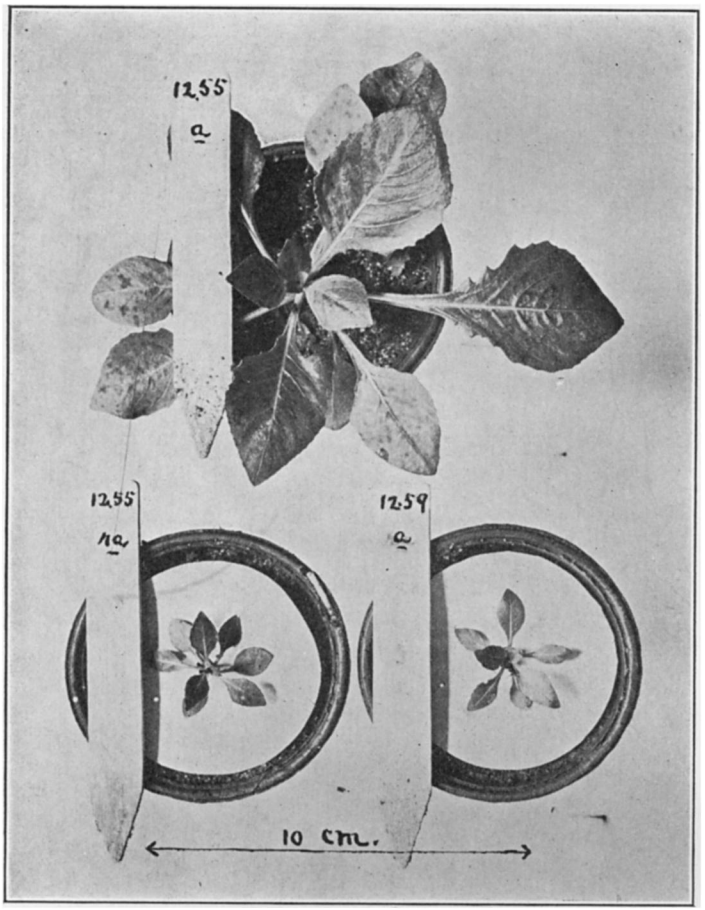


FIG. 7. Rosettes in the F_3: 12.55*a* representative of the mass of the culture from the F_2 plant 11.42*f* (Fig. 6); 12.55*ra* a sister rosette, one of 8 dwarfs in the same culture; 12.59*a* a rosette from a plant similar to 11.42*r* (Fig. 5).

but must not be regarded as representing a class since its characters intergraded through numbers of plants into the mass of the culture. The contents of one selfed capsule, 219 seeds, were sown as culture 12.55; these produced 75 seedlings from which 62 rosettes developed.

From the mass of rosettes with characters as illustrated in Fig. 7, 12.55*a*, a group of 8 dwarfs (Fig. 7, 12.55*ra*) was quickly recognized. One can hardly imagine a much sharper contrast between rosettes in the same culture than is shown in this illustration (Fig. 7, 12.55*ra* compared with 12.55*a*). By the side of the dwarf 12.55*ra* is a rosette, 12.59*a*, of the F_3 from one of the dwarfs of the F_2, 11.42*ra* (similar to Fig. 5). A comparison will show how perfectly the F_2 type 11.42*f* (Fig. 6) has repeated the behavior of its parent hybrid F_1 plant 10.30*Lb* in throwing off a class of similar dwarfs. The 8 dwarfs of the culture 12.55 were set out under conditions ill-suited to their constitution and I had great difficulty in saving 5 plants from a period of drought. These are now in the hot house, where it is hoped that they may be brought to maturity.[2]

The normal rosettes of the F_3 culture 12.55, excluding the 8 dwarfs described above, developed a fairly uniform set of plants which at maturity exhibited a foliage of broader and more crinkled leaves than those of the F_2 parent hybrid 11.42*f*. This progressive advance in foliage was also supplemented by a greater vigor and size of the plants, although the flowers remained without marked change. Summarizing the behavior of the F_2 plant 11.42*f* in the F_3 generation, the most striking points were the repetition of the behavior of the F_1 parent hybrid 10.30*Lb* in throwing off the same types of dwarfs, and a much greater uniformity among the normal plants with apparent advance in leaf size and vegetative vigor.

The next form to be considered is a plant, 11.42*g*, which was fairly representative of the mass of the F_2 generation from 10.30*Lb*. This plant (Davis, '12*a*, p. 415, 11.42*g*) was 1.5 m. high and characterized by large flowers (petals about 4 cm. long) and large crinkled leaves (Fig. 8). It was a type rather common and intergrading with other forms of the culture. It exhibited a decided progressive advance in flower and leaf size over the F_1

[2] Of the 5 dwarfs 3 are now (June 1, 1913) almost full grown and true to the type.

parent plant 10.30*Lb*, but stood close to the center around which the mass of the F_2 culture varied.

From this plant, 11.42*g* (Fig. 8), the contents of two

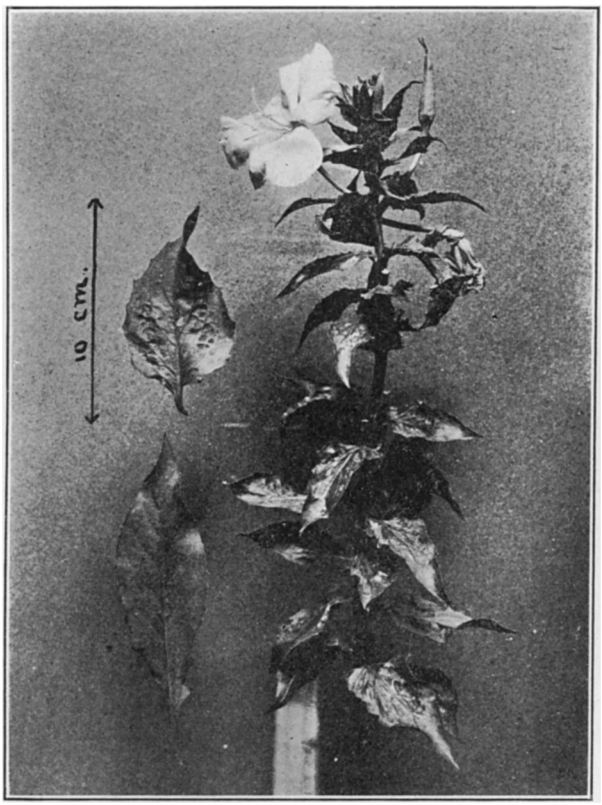
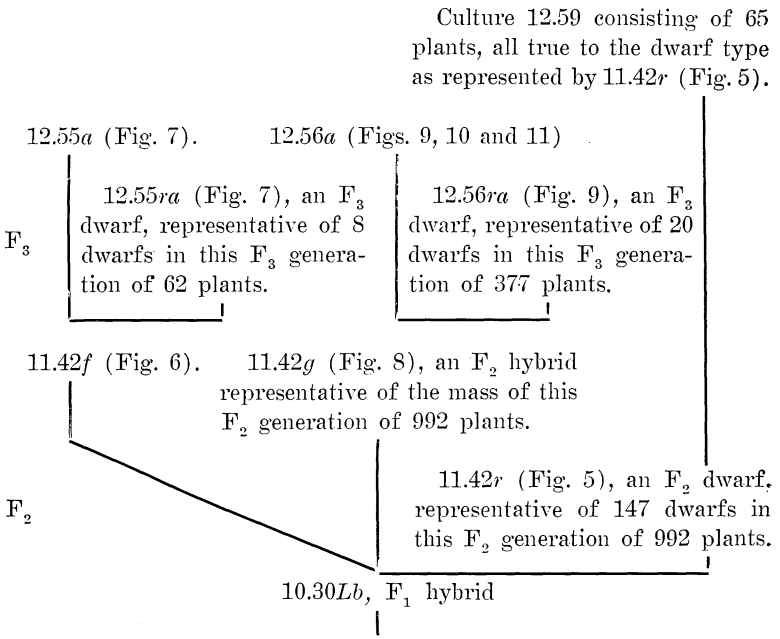


FIG. 8. A type, 11.42*g*, representative of the mass of the F_2 generation from the F_1 plant 10.30*Lb*, hybrid of *grandiflora* $B \times$ *biennis* A. A form characterized by large, crinkled leaves and large flowers (petals 4 cm. long).

capsules, about 900 seeds, were sown (culture 12.56) and 377 rosettes developed. Among the rosettes a group of 20 dwarfs very shortly defined itself. The characters of the dwarfs are illustrated in Fig. 9, 12.56*ra*, where they may be compared with those of a normal rosette, 12.56*a*, shown above. The same sort of contrast is here exhibited as that illustrated by Fig. 7 for the culture from 11.42*f*. By the side of the dwarf 12.56*ra* is again figured the

rosette 12.59*a* (compare Fig. 9 with Fig. 7) of the F_3 from one of the dwarfs in the F_2, 11.42*ra* (similar to Fig. 5). Figs. 7 and 9 then illustrate the same behavior, in the first case that of the F_2 plant 11.42*f*, and in the second case that of the F_2 sister plant 11.42*g*, and both plants have produced a class of dwarfs similar to that which appeared in the F_2 11.42*r*, the type shown in Fig. 5. I had the same difficulty with the 20 dwarfs from 11.42*g* as with the 8 from 11.42*f* and was only able to save 7 plants from a period of drought. These at the present writing are also in the hothouse, where they bid fair to reach maturity.[3]

An outline of the genealogy of the sets of dwarfs produced by the family from the F_1 hybrid 10.30*Lb* will make clearer its complications. The important feature is of course the close parallelism of this history with the behavior of *Lamarckiana* when it produces in successive generations a marked variant that breeds true.



[3] Of the 7 dwarfs 4 are now (June 1, 1913) almost full grown and true to the type.

Of the 357 normal green rosettes in culture 12.56 from 11.42*g*, 128 plants were set out and brought to maturity. A single interesting rosette with leaves sharply streaked with white failed to live. The rosettes consisted of unusually broad, ovate or elliptical leaves, loosely arranged (see Fig. 9, 12.56*a*). The group of plants at maturity

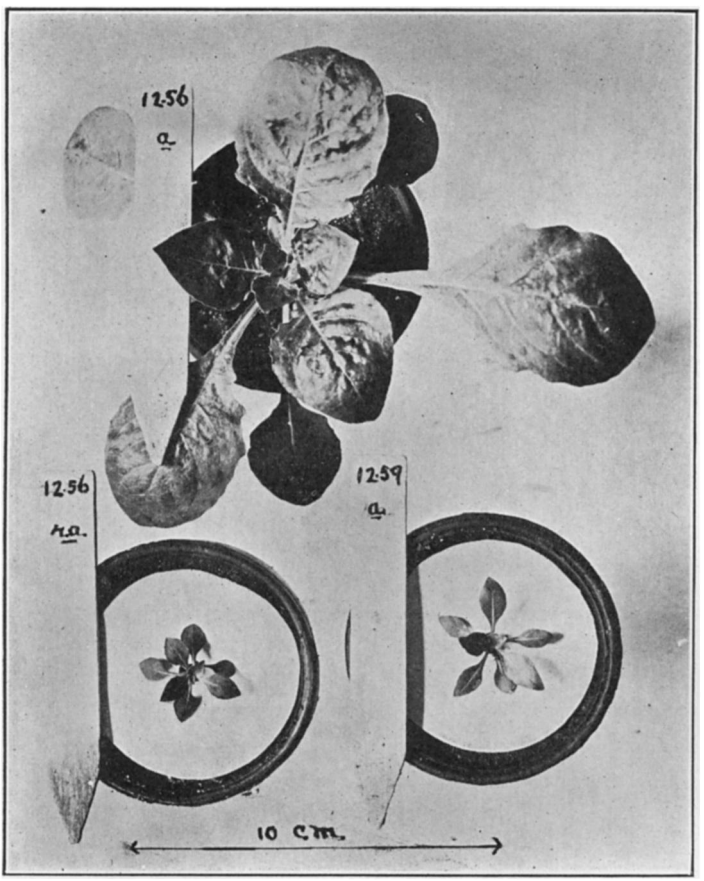


FIG. 9. Rosettes in the F_3: 12.56*a* representative of the mass of the culture from the F_2 plant 11.42*g* (Fig. 8); 12.56*ra* a sister rosette, one of 20 dwarfs in the same culture; 12.59*a* a rosette from a plant similar to 11.42*r* (Fig. 5).

exhibited a range of variation in flower and leaf size, but on the whole was remarkably uniform except for the plant 12.56*x* to be described later.

The type characteristic of this group (culture 12.56) is one of the most interesting among my hybrids and will be

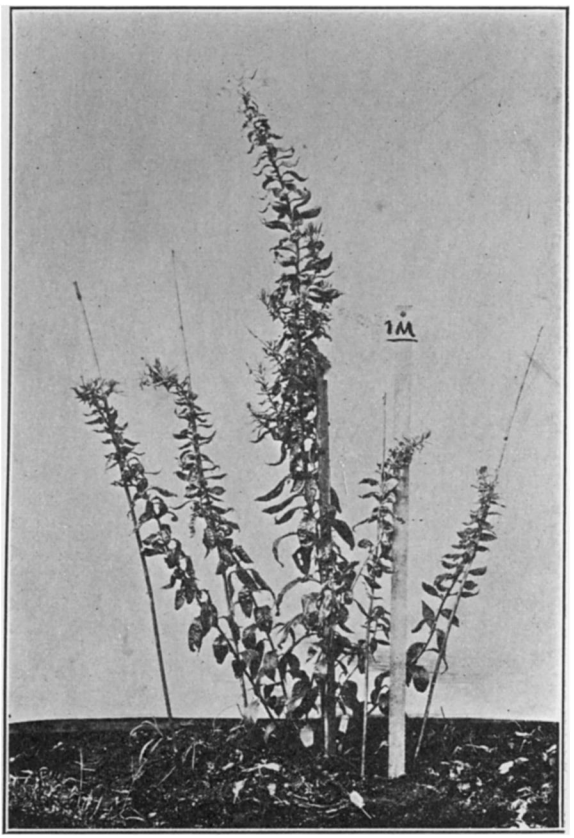


FIG. 10. Mature plant, 12.56*a*, from the rosette 12.56*a* (Fig. 9), representative of the mass of the F_3 generation from the F_2 hybrid 11.42*g* (Fig. 8). A form remarkable for the size and thickness of the leaves, size of flowers and general vigor.

briefly described. It is a large plant, 1.5–2 m. high, with long branches from the base (Fig. 10), stem green above, reddish below, leaves much larger and thicker than in *grandiflora,* and strongly crinkled. Inflorescence (Fig. 11) *grandiflora*-like, very dense on the main branches, bracts persistent. Buds 8–9 cm. long, cone circular in section, sepals green, their tips attenuate. Petals about

4 cm. long. Stigma 5–8 mm. above the tips of the anthers. Capsules 2.8 cm. long.

Although this type presented many of the peculiarities of the *grandiflora* parent, there was evident a remarkable

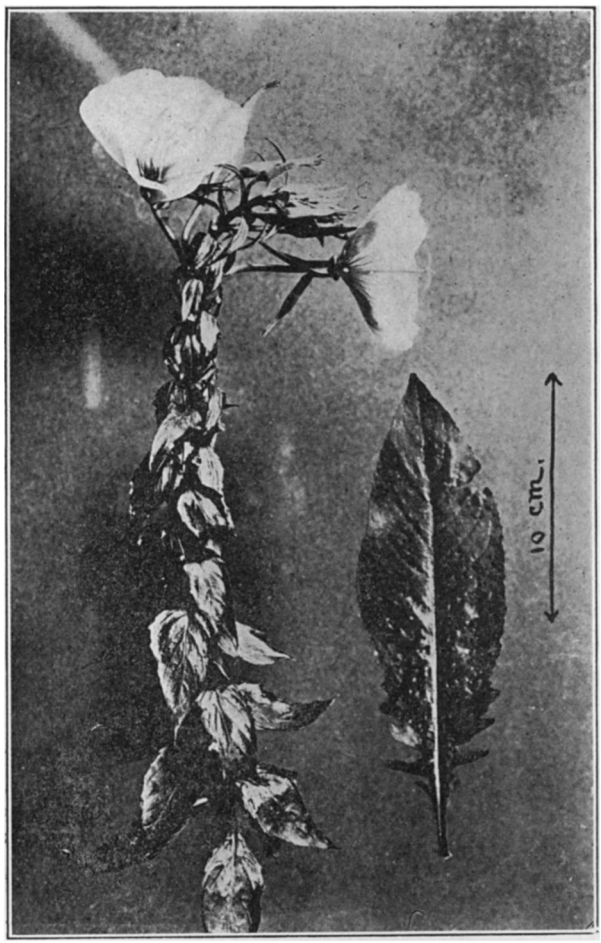


FIG. 11. Flowering side branch of the F_3 hybrid 12.56*a* (Fig. 10), showing the *grandiflora*-like inflorescence and broad crinkled bracts. At the right is a leaf from the lower portion of the main stem.

degree of progressive evolution in the size and thickness of the leaves, size of the flowers, and general vigor. These progressive advances introduce characteristics of

Lamarckiana and make this type a very favorable one for back crossing with certain races of *biennis* which in certain respects (*e. g.*, stem coloration, rosette characters, etc.) are closer to *Lamarckiana*. Such a back cross was made last summer with *biennis D* and should result in a further advance towards the synthesis of *Lamarckiana*-like hybrids between *grandiflora* and forms of *biennis*.

The single plant, designated 12.56*x* in the culture de-

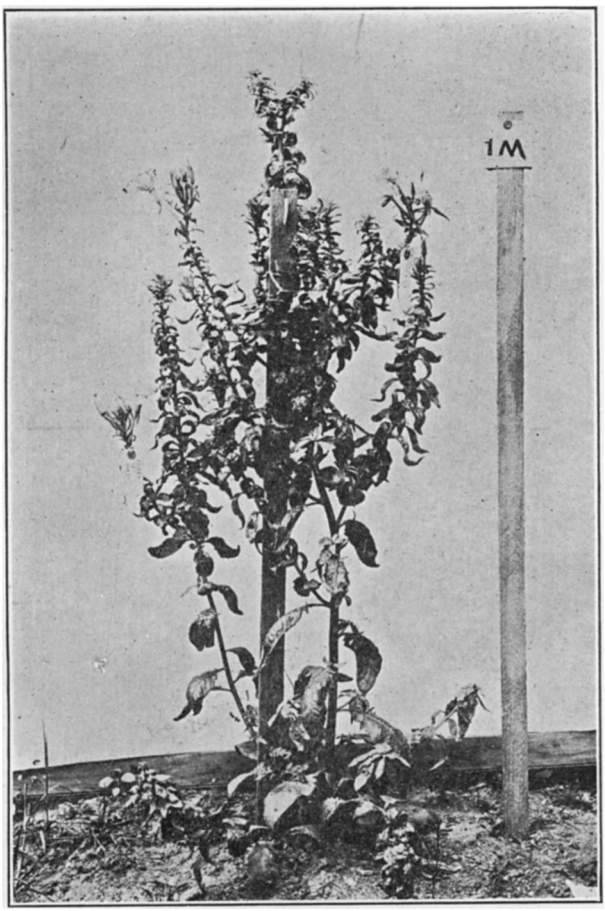


FIG. 12. Mature plant, 12.56*x*, a remarkable type represented by a single individual in the F_3 from the F_2 hybrid 11.42*g* (Fig. 8). A form distinguished by its stocky habit and very large thick leaves. The plant had at least 21 chromosomes, the triploid number.

scribed above, presented characters that distinguished it from the mass in much the same way that *gigas* is distinguished from *Lamarckiana*. In the rosette stage the plant was marked because of the exceptional thickness and large size of the leaves. The mature plant, somewhat more than 1 m. high (Fig. 12), was much shorter

FIG. 13. Flowering side shoot of the F_3 hybrid 12.56α (Fig. 12), showing the four-angled buds, and dense inflorescence, flat-topped because of the short internodes. At the right is a leaf from the lower portion of the main stem.

and more stocky (*gigas*-like) than the average of the culture; the leaves were even thicker. The inflorescence (Fig. 13) was more dense because of the shorter internodes so that the top appeared flattened as in *gigas*.

The buds, 8–9 cm. long, presented a stouter cone, 4-angled, and the sepal tips were less attenuate and thicker. The petals were about 4 cm. long, the hypanthium was shorter, and the stigma lobes, 4–6 mm. above the tips of the anthers, were thicker than in the type representative of the mass of the culture. The capsules, 1.8 cm. long, were shorter and stouter. So many of these points of difference suggest the characteristics of *gigas* that it was not surprising to find the chromosome count to be above 14, the normal diploid number for *Œnothera*. It is difficult to determine the exact number, but from counts made this spring at the growing points of seedlings from this plant I am certain that the chromosome count is at least as high as 21, the triploid number. It will be remembered that the triploid number has been determined by both Miss Lutz ('12) and Stomps ('12) for "mutants" derived from *lata* and *Lamarckiana* to which Stomps has given the name *semi-gigas*. We have then in this plant (12.56*x*) a variant from the parent hybrid which probably corresponds closely to the "triploid mutants" of *Lamarckiana* or its derivatives.

There will now be briefly described the F_3 generation from a type 11.42*l*, represented by a single plant in the F_2 from 10.30*Lb* (Davis, '12*a*, p. 415, 11.42*l*). This plant, about 1 m. high, was remarkable for its broad, entire, much-crinkled leaves (Fig. 14); the flowers were medium-sized (petals 2 cm. long). The contents of two capsules, 222 seeds, were sown, from which 117 plants were obtained and brought to maturity (culture 12.58). The mass of the rosettes consisted of broad elliptical leaves, crinkled and loosely arranged. Several rosettes were *grandiflora*-like, intergrading, however, with the mass, and 8 presented a long narrow form of leaf. The culture at maturity was very well graded from plants 1.6 m. high, with flowers as large as those of *grandiflora* (petals 3.5 cm. long) to plants the counterpart of the F_2 parent hybrid 11.42*l*. The foliage of the culture as a whole continued the progressive advance of 11.42*l* as shown by

larger leaves which were more strongly crinkled. The plants from the 8 rosettes with narrow leaves also had at

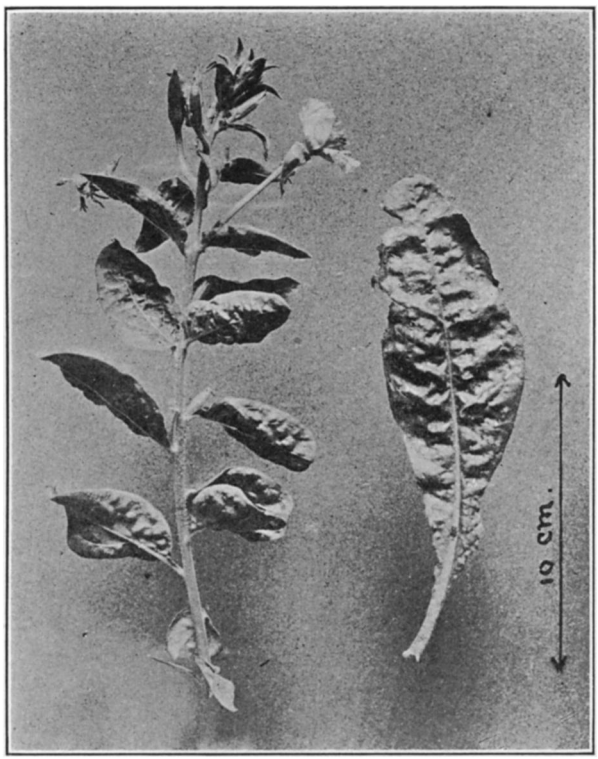


FIG. 14. A type, 11.42*l*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora* $B \times$ *biennis* A, represented by a single plant. A form characterized by its broad, entire, much crinkled leaves and medium-sized flowers (petals 2 cm. long).

maturity smaller and narrower leaves; the flowers were medium-sized (petals 2.5 cm. long). They constituted a clearly defined group but could not be called dwarfs. It is interesting to note that an F_2 type so clearly defined as 11.42*l* may, nevertheless, be strongly heterozygous and consequently may be very far from representing a stable segregate in the F_2.

A remarkable plant, 11.42*j*, appeared in the F_2 from 10.30*Lb* (Davis, '12*a*, p. 415, 11.42*j*) which in habit and

foliage agreed very closely with the "mutant" *Œnothera elliptica* obtained by De Vries ('01, vol. I, pp. 280–284) from *Lamarckiana*. This plant, 7 dm. high, developed from a rosette with narrow leaves and at maturity presented a foliage of very narrow leaves well illustrated in

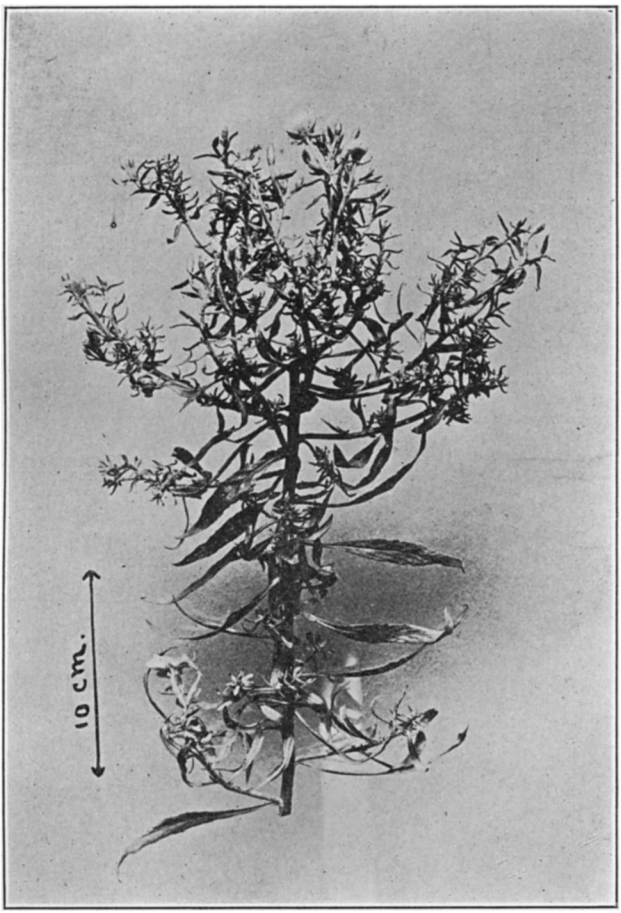


FIG. 15. A type, 11.42*j*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*, represented by a single plant. A remarkable form with a foliage of very narrow leaves, and with very small flowers (petals 6 mm. long), anthers sterile. This plant in its habit and foliage matched closely De Vries's "mutant" *Œnothera elliptica*.

Fig. 15, which shows the top of the main stem. The

flowers, however, were very small (petals 6 mm. long) and the anthers as far as observed were completely sterile. Since this plant apparently could not be selfed, I pollinated it from a large sister plant of the F_2 with *grandiflora*-like flowers. The result was 154 seeds from several capsules which gave 46 plants in the F_3 generation (culture 12.57). Of the rosettes, 40 proved to be large-leaved, exhibiting much variation, but with several plants similar to *grandiflora;* 6 rosettes bore long narrow leaves.

From the 40 large-leaved rosettes there developed plants 1.2–1.5 m. high with a foliage of crinkled leaves, and medium-sized flowers (petals 2–2.5 cm. long). Of the 6 narrow-leaved rosettes, 5 developed plants which agreed with the "*elliptica*" type and 1 became a broad-leaved form similar to the 40 described above. The 41 large-leaved plants of the culture evidently took their characteristics largely from the pollen parent of the cross and represented something of a blend. I am at a loss to account for the five individuals of the "*elliptica*" type unless they came from apogamously formed seed. The "*elliptica*" type has since appeared in other F_2 generations from the cross *grandiflora* × *biennis,* and it appears to be a not uncommon expression of one of the extreme forms which may be thrown in the F_2 of this cross.

(*To be continued*)